The role of resting eggs in the recovery of zooplankton community in a marginal lake of the Paranapanema River (São Paulo, Brazil), after a long drought period

O papel dos ovos de resistência na restauração da comunidade zooplanctônica num lago marginal ao Rio Paranapanema (São Paulo, Brasil), após um período prolongado de seca

Panarelli, EA.[1], Casanova, SMC.[2] and Henry, R.[2]

[1]Universidade Estadual do Matro Grosso do Sul – UEMS,
Rua Pereira Gomes, 355, Vila Santa Maria, CEP 79400-000, Coxim, MS, Brazil
e-mail: epanarelli@ig.com.br

[2]Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista – UNESP,
Campus de Botucatu, Rubião Jr., s/nº, CEP 18618-000, Botucatu, SP, Brazil
e-mail: casanova@ibb.unesp.br; rhenry@ibb.unesp.br

Abstract: The dynamics of the zooplankton community of Cavalos Lake (a lateral lake to the Paranapanema River) was studied during, previously and after a severe drought period (from March 2000 to December 2001). Dry sediment was collected in order to investigate the importance of resting eggs in the recolonization of the ecosystem. During the drought period, a richness of 39 species was noticed. An increase to 49 species was found in the beginning of lake recovery and, the highest richness (67 species) was recorded from June to December 2001, when a hydrological stability was attained in the lake. At the end of the study, species richness and diversity presented values similar to data of the period before drought. Although, some alterations in composition were recorded: Rotifera presented a higher species number at the end of study; Cladocera richness was reduced to half of the species number found in the period before the drought. Significant changes on densities were reported for Copepoda, with higher abundance being recorded in the period of higher hydrological stability in the lake. Hatching experiment showed that the sediment of Cavalos Lake presents a great amount of diapausing organisms, despite that only 14 species hatched during the laboratory study. The recovery of zooplankton community occurred mainly due to resting eggs present in sediment, since the lake did not receive water from river during the period of this study.

Keywords: zooplankton, lateral lake, resting eggs, drought period, Paranapanema River.

Resumo: A dinâmica da comunidade zooplanctônica da Lagoa dos Cavalos (um lago lateral ao Rio Paranapanema) foi estudada durante, previamente e posteriormente a um período severo de seca (de março 2000 a dezembro 2001). Sedimento seco foi coletado para investigar a importância dos ovos de resistência na recolonização do ecossistema. Durante o período de seca, uma riqueza de 39 espécies foi registrada. Um aumento para 49 espécies foi encontrado no início da restauração do lago e, a mais alta riqueza (67 espécies) foi registrada de junho a dezembro de 2001, quando estabilidade hidrológica foi atingida no lago. No término do estudo, a riqueza e a diversidade de espécies apresentaram valores similares aos dados do período anterior à seca. Embora, algumas alterações na composição foram registradas. Rotifera apresentou um número mais alto de espécies no final do estudo; a riqueza de Cladocera foi reduzida à metade no número de espécies encontrado no período anterior à seca. Mudanças significativas nas densidades foram registradas para Copepoda, com a mais alta abundância sendo registrada no período de maior estabilidade hidrológica no lago. O experimento de eclosão mostrou que o sedimento da Lagoa dos Cavalos apresenta uma grande quantidade de organismos em diapausa, a despeito de que somente 14 espécies eclodiram durante o estudo de laboratório. A restauração da comunidade zooplanctônica foi devida principalmente aos ovos de resistência presentes no sedimento, visto que o lago não recebeu água do rio durante o período deste estudo.

Palavras-chave: zooplâncton, lagoa lateral, ovos de resistência, período de seca, Rio Paranapanema.

1. Introduction

In perennial aquatic environments, the occurrence of long and intense drought periods, sometimes with the disappearance of aquatic systems, can be a catastrophic event. According to Harper (1977), catastrophic events had selective consequences, since a modification on community structure and, local extinction of some populations can occur. Conversely, in those conditions, many species are inducted to come into dormancy in response to extreme environmental alterations. In this way, many plant and animal species can perform "dispersion" or a "migration through time" (Begon et al., 1996).

After a long drought period, the recovery of zooplankton community can be very fast, since the organisms can remain in a diapausing phase for a long period of time and in very adverse environmental conditions, and can return to active phase when the conditions are favorable. However, the community composition and structure after the drought can be very distinct from the previous situation, because after the beginning of succession, the physical and chemical conditions of the water are usually different from the previous situation. Thus, the dormancy interruption for different species in sediment can occur in distinct periods and proportions.

Dormancy interruption promoting factors are yet unknown and can vary according to species. Chartterjee and Gopal (1998) believe that temperature, photoperiod, light intensity, and carbon dioxide concentration are some of the factors that can induce the hatching of resting eggs. According to De Stasio (1989, 1990), the dormancy interruption of zooplankton eggs on Bullhead Pond (Rhode Island, USA) is related to abiotic factors, such as photoperiod and dissolved oxygen concentration, biological interactions, and intense fish predation. According to Hairston et al. (1995), the time necessary for resting eggs to hatch is related to environmental variables as well as the time that the eggs remained in dormancy.

Many eggs do not hatch during the first episode of inundation after the drought; the persistence of organisms in dormancy after successive episodes of inundation suggests that the exigencies for dormancy interruption are diverse and complex (Brock et al., 2003). Thus, an "egg bank" on sediment is a frequent occurrence. This expression is similar to a "seed bank" and it is used as a stock of resting forms produced in different periods of time (De Stasio, 1989). Hairston et al. (1995), when comparing "seed banks" studies, showed the importance of "egg banks" as a stock of genetic variability of organisms having a considerable role on ecological and evolutionary processes.

In the present work, the zooplankton of an isolated lake, marginal to a river, was studied in four periods: previously to a drought; during the drought, when an ephemeral episode of water accumulation occurred in the lake and a hatching experiment of resting eggs was conducted; in the initial phase of lake recovery and, during the hydrological stability of the lake, after the drought. In order to have a better understanding of the recovery of zooplankton community, the aims of this study were: a) to characterize the physical and chemical variables of the aquatic system; b) to record changes on community structure during the study period; c) to analyze the recovery process of zooplanktonic populations after the end of drought, and d) to point out the existence of latent forms on lake sediment following the hatching of resting eggs in laboratory. Thus, the following questions were proposed: 1) Hatching of resting eggs, after a prolonged drought, promotes the recovery of zooplankton diversity in a lacustrine isolated environment?; 2) The zooplankton community composition and structure show a significant difference, when compared before and after prolonged drought?

2. Material and Methods

2.1. Study area

Cavalos Lake is located laterally to Paranapanema River in its mouth zone into Jurumirim Reservoir (23° 27' 30" and 23° 30' 00" S, and 48° 36' 50" and 48° 38' 29" W), in the southeast region of São Paulo State, Brazil (Figure 1a). The lake presents no communication with the river during the year. However, during episodes of extremely high water level, as it was observed in February 1997 and 2004, an exchange of surface water and biota occurs.

Cavalos Lake is a perennial environment, being fed by rains or by water flux from the river through the hyporrheic zone. However, a long and intense drought period led to the lake disappearance during eight months (from June/00 to Jan./01), and a colonization of terrestrial vegetation, mainly gramineous, was noticed on the exposed sediment. Henry (2005) mentioned that, after the damming of waters in Jurumirim, similar drought episodes were observed in 1969, 1976, and 1986.

During the study period, no connection between the lake and the river was observed; thus, the probable forms of the recovery of the zooplankton community are due to activity return of dormancy forms from the "egg bank" on sediment, or introduced by wind and birds. The zooplanktonic populations of Cavalos Lake was previously studied by Martins and Henry (2004), that presented data relative to quarterly samplings conducted from December 1998 to December 1999, before the drought.

2.2. Morphometric variables

A bathymetric study was conducted on July 13, 2001 after the long drought period. The depth determinations were made through manual soundings with the boat in movement, in nine transects perpendicular to the maximum length of the lake. Hypsographic curves of area and volume were made and, the morphometric parameters were calculated according to Von Sperling (1999). The lake volume was estimated for each sampling month, according to the maximum depth variation plotted on the respective hypsographic curve.

2.3. Environmental parameters

An analysis of the variation of abiotic factors was performed from March 2000 to December 2001 in three sampling stations (P1, P2 and P3; Figure 1c). The following variables were evaluated: pluviosity (data obtained in the climatological station of Angatuba town); air and water temperature (by a Toho Dentam ET-3 thermistor);

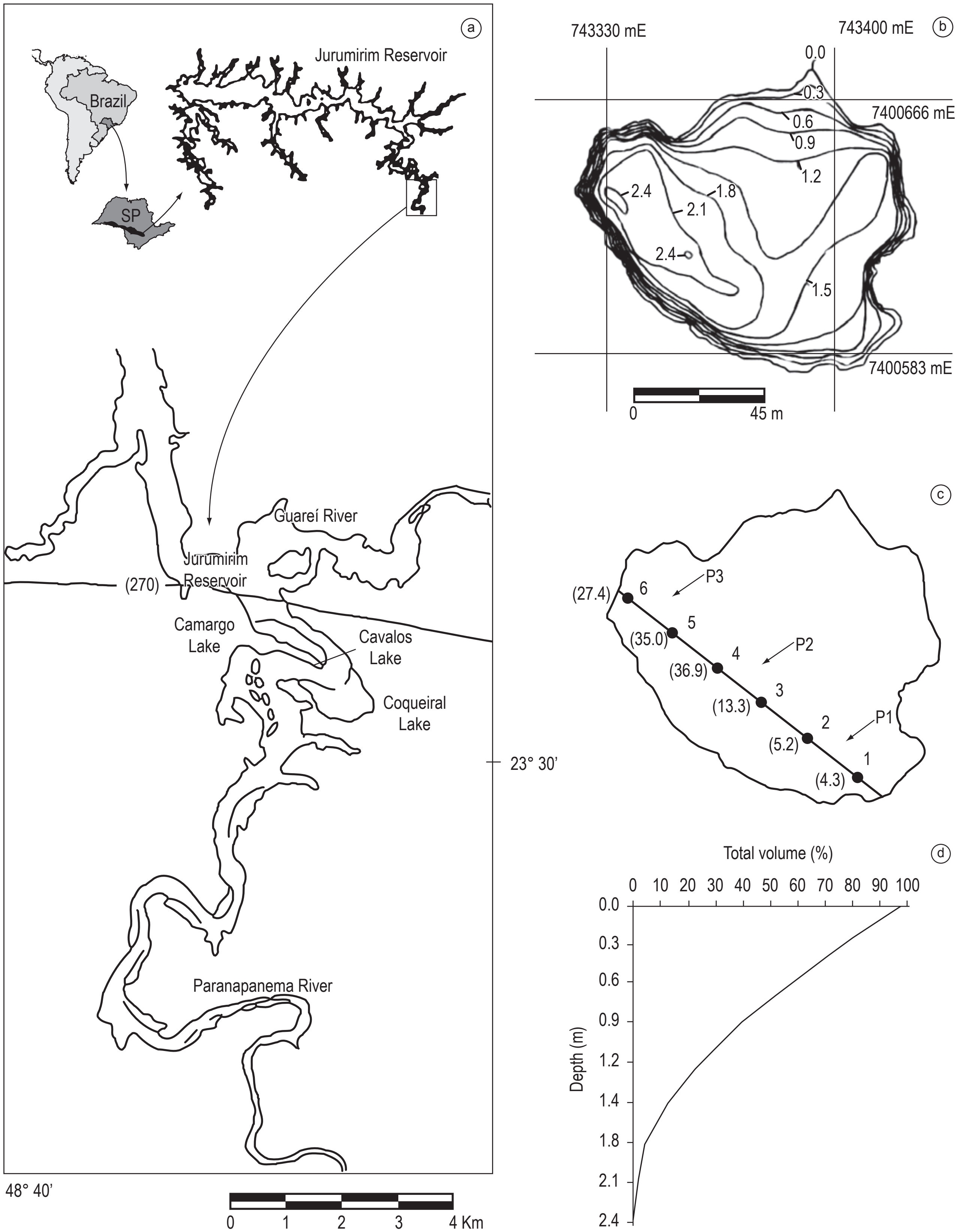

Figure 1. a) Location of Cavalos Lake; b) Bathymetric map; c) P1 to P3: sampling stations of zooplanktonic organisms (1 to 6: sites for sediment sampling, water content (%) in parentheses); d) Hypsographic curve of total volume in relation to maximum depth.

water transparency (by a Secchi disk); dissolved oxygen (by the Winkler method, Golterman et al., 1978); pH (by a Micronal B-380 pHmeter); electric conductivity (by a Hatch model 2511 conductivimeter, data corrected to 25 °C, Golterman et al., 1978); total, organic and inorganic suspended matter (by the gravimetric method, according to Cole, 1979) and phytoplankton biomass (total pigments) (according to Golterman et al., 1978).

2.4. Zooplankton analysis

The zooplanktonic organisms were collected with a bucket or a becker from the lake surface when the depth was <0.5 m. When the lake presented a depth > 0.5 m, all the water column was sampled with a suction bomb (Still P835) using a tube of 1.5 inch diameter. The water volume was filtered in a 50 µm mesh net and, ranged from 5 to 100 L. After that, the samples were fixed in 4% formaldehyde.

In laboratory, the individuals of Cladocera and, copepodids and adults of Copepoda were counted in a checkered chamber using a stereoscopic microscopy and, densities were expressed in organisms m^{-3}. For nauplii of Copepoda and Rotifera organisms, it was used a Sedgwick-Rafter chamber under an optical microscopy. At least 150 organisms per sample were counted.

Species identification was performed according to Koste (1978a, 1978b); Loureiro (1997); Pontin (1978); Reid (1985) and Rocha and Matsumura-Tundisi (1976).

2.5. Hatching experiment of resting eggs

During the lake extinction period, sediment sampling was performed on September 2000 in 6 equidistant sites inserted in a transect parallel to the maximum axis of the lake (Figure 1c) in order to conduct a hatching experiment of resting eggs. The water content in sediment was estimated through the difference between initial and final dry weight (in oven at 60 °C, during 72 hours).

Sediment samples were collected with a plastic cylindrical tube (75 cm^3 volume). In laboratory, three sediment sub-samples (5 g) of each site were disposed in beckers containing distilled water (50 mL) and were incubated at 22 °C. During the first week of incubation, the water was filtered each two days in a 55 µm mesh net. After the eighth day, the filtration was made weekly during two months. Organisms retained in the net were transferred to flaks, fixed in 4% formaldehyde, after being identified, and counted. The methodology used in this experiment was adopted from Crispim and Watanabe (2000).

In the day after the sediment sampling, a rain episode (43.7 mm on September 12, 2000) produced a water puddle in site 3 (Figure 1). Water was collected from this site in order to observe zooplankton organisms, which hatched after 6 hours of water accumulation.

2.6. Quantitative analysis of zooplankton

The Shannon-Wiener index was used for diversity computation and equitability was estimated through the diversity and maximum diversity ratio (Krebs, 1998).

Relationships between environmental variables and densities of zooplankton organisms were determined through Spearman correlations (P > 0.05). Only taxa with frequency of occurrence >20% were considered.

In order to determine similarity of abiotic variables among months (from March 2000 to December 2001), a similarity analysis was conducted using the grouping method by unweighted pair-group average and the Euclidean distance as a distance coefficient through Statistica program (4.2 version).

3. Results

3.1. Physical and chemical characterization of Cavalos Lake

Cavalos Lake is a shallow and relatively small environment, with a practically circular shape (Figure 1, Table 1).

Drought was severe (pluviosity < 100 mm, Figure 2), for the majority of 2000 year. From November 2000 to March 2001, rain was intense (precipitation ranging from 150 to 250 mm). From April (90 mm) to August 2001 (50 mm), the precipitation first decreased, increasing at the end of study (178 mm in December 2001).

The lowest water temperatures were observed from May to September 2001 (range: 14-22 °C) and the highest, from Nov./00 to Feb//01 (range: 26-28 °C) (Figure 2).

Maximum depth and volume of the lake decreased progressively in the first months of study (Figure 3). From June on, the lake disappeared completely, remaining without water until January 2001. In September 2000, an ephemeral water accumulation was recorded at the maximum depth of

Table 1. Morphometric parameters of Cavalos Lake.

Primary morphometric parameters		Secondary morphometric parameters	
Maximum length (m)	127.3	Mean depth (m)	1.35
Maximum depth (m)	2.4	Mean width (m)	67.5
Maximum width (m)	103.5	Shoreline index	1.27
Perimeter (m)	416.4	Volume development index	1.69
Surface area (m^2)	8592.5	Relative depth (%)	2.30
Volume (m^3)	11622.7	Mean declivity (%)	0.7

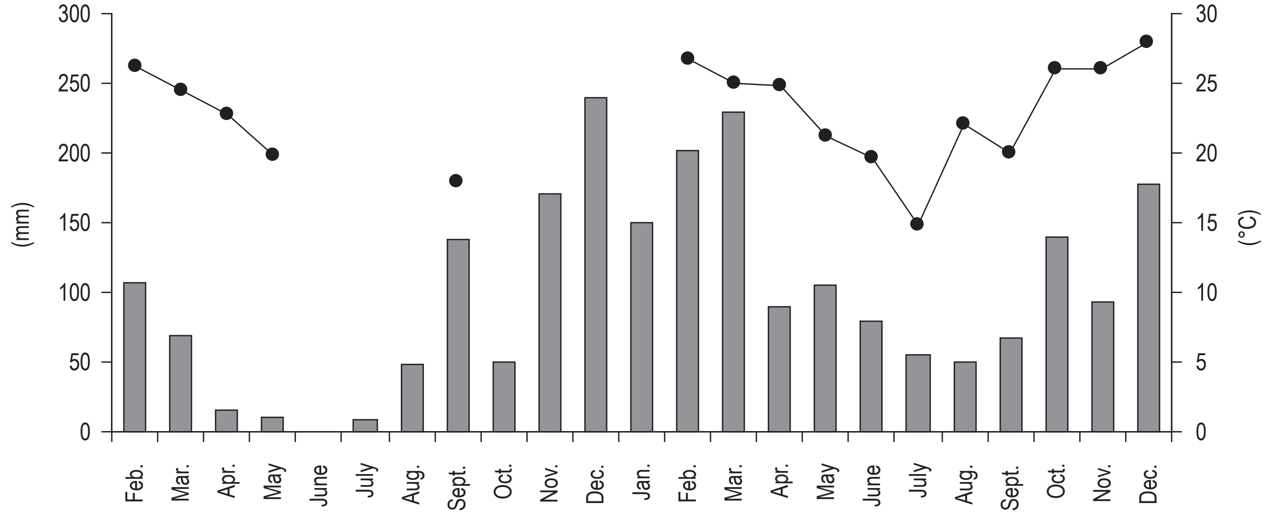

Figure 2. Monthly accumulated rain precipitation (in bars) in Angatuba region and water temperature (line) at surface of Cavalos Lake during the study period.

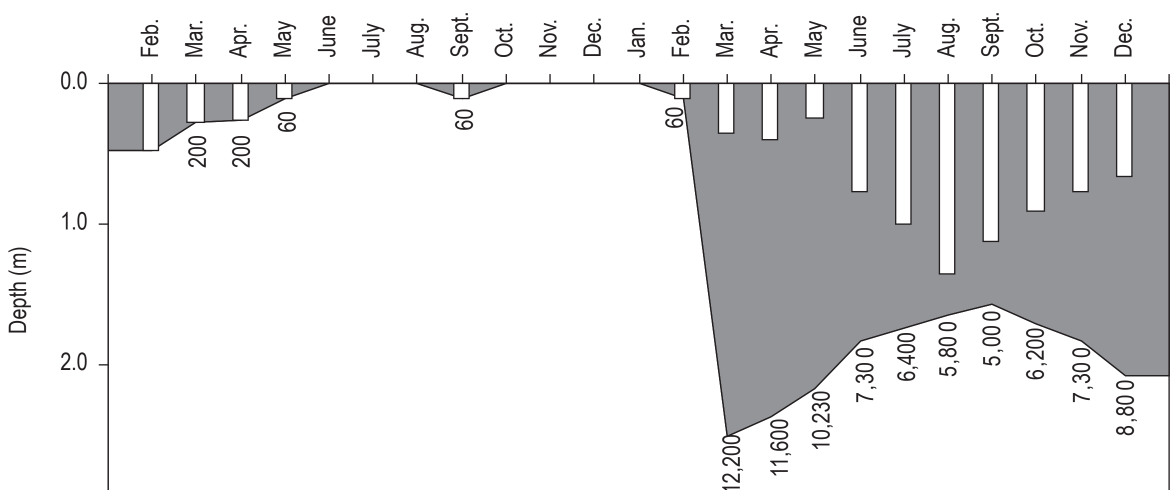

Figure 3. Mean depth (in gray) and water transparency (in bars) and, estimated volume (in m^3) of Cavalos Lake from February 2000 to December 2001.

the lake. Despite the increase on pluviosity from November 2000, the lake recovery began only in February 2001. In March, the lake reached a 2.5 m depth and a volume of 12,200 m^3.

During 2000, the water transparency reached the lake bottom and, from February 2001 on, the Secchi disk values decreased with the increase of pluviosity (Figure 3).

Suspended matter values were very high two months before lake extinction, inorganic fraction represented > 70% (Figure 4). For the other months, values did not exceed 50 mg.L^{-1} and, from July 2001 on the concentrations decreased. During the first six months after lake filling, suspended matter was composed by organic particles. From August 2001 on, the inorganic fraction predominated up to the end of study (Figure 4).

Dissolved oxygen contents (from 79 to 89% saturation) were higher in the period before lake disappearance, when a slow decrease of pH was recorded (Figure 5). In the initial phase of lake filling, the oxygen concentration was very low (< 2.0 mg.L^{-1}; from 0.0 to 3.4% saturation). Then, dissolved oxygen increased, but the concentration did not exceed 6.0 mg L^{-1} (< 80% saturation). In this period, com water pH was slightly acid (Figure 5), and water conductivity was relatively high (Figure 6).

Total pigments showed high values on March 2001 (168 µg.L^{-1}), followed by a great reduction and, from August 2001 on, the concentration did not exceed 3 µg.L^{-1} (Figure 6).

The grouping analysis shaped two groups of distinct months in relation to environmental variables, showing

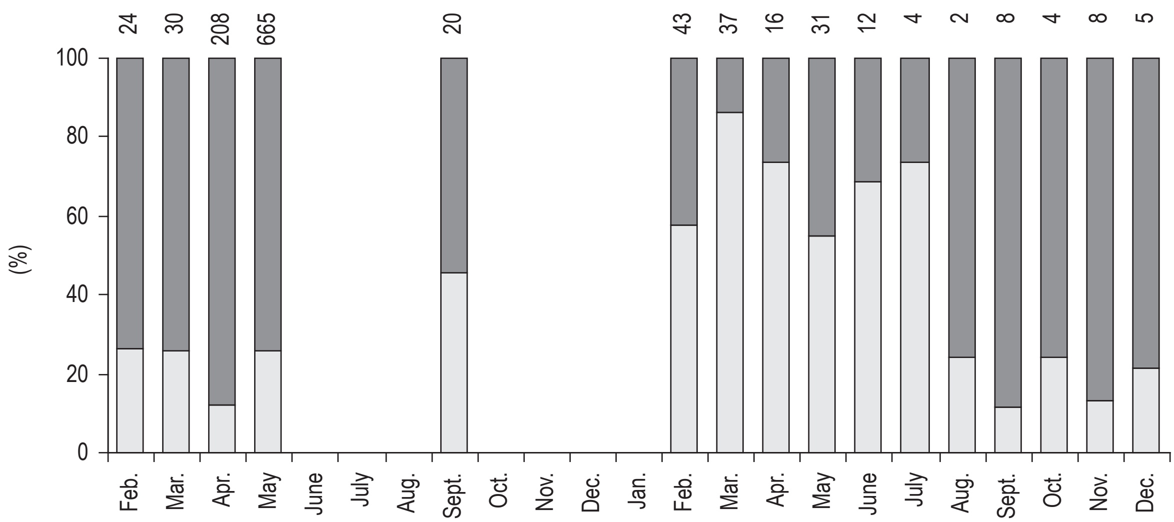

Figure 4. Ratios (in %) between organic (in gray) and inorganic (in black) contents of suspended matter (total values above each bar, in mg L^{-1}) in Cavalos Lake from February 2000 to December 2001.

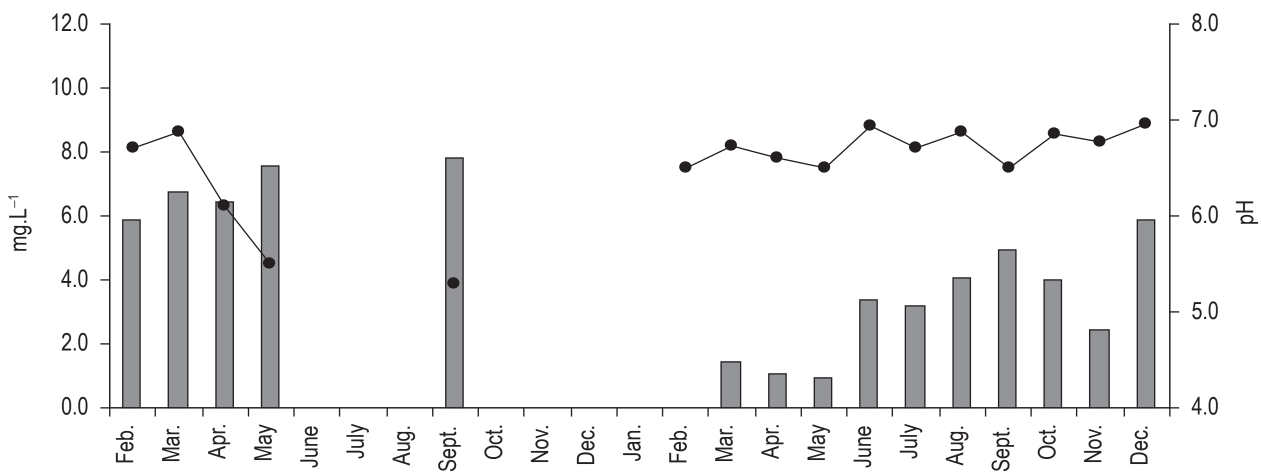

Figure 5. pH (line) and dissolved oxygen (mg L^{-1}; bars) in Cavalos Lake from February 2000 to December 2001.

the biggest similarity from March 2000 to February 2001, corresponding to low water volumes and depths, and high inorganic ratios in suspended matter (Figure 7). From March to December 2001 corresponds to the period after lake recovery. However, in this period it was noticed a lower similarity of water characteristics between March and April when compared to other months, when higher values of water volume were found. From June to November 2001, reductions on pluviosity and suspended matter, with consequent increase on water transparency, were the determinant factors of similarity.

3.2. Zooplankton structure

Cavalos Lake presented a relatively high richness of zooplankton taxa (Table 2). A total of 90 species was recorded during all the study. Rotifera presented the highest richness (59 taxa), followed by Cladocera (21 taxa) and Copepoda (10 taxa). The highest values of richness of Rotifera were recorded in March, June and September, 2001. Before lake extinction (in March and April 2000), the highest values of richness were found for Cladocera (7 species). Copepoda presented the highest richness of species in August and September 2001.

In the hatching experiment of resting eggs, it was recorded 14 taxa of Rotifera, Cladocera and Copepoda. Two Rotifera taxa not found in the other phase of study, *Lecane inermis* (Bryce, 1892) and *Philodina* Ehrenberg, 1830, hatched in laboratory. In September 2000, during the temporary water accumulation in lake, only 9 species were recorded.

Comparing the relative abundance of zooplanktonic groups (Table 3), Rotifera predominated in the majority

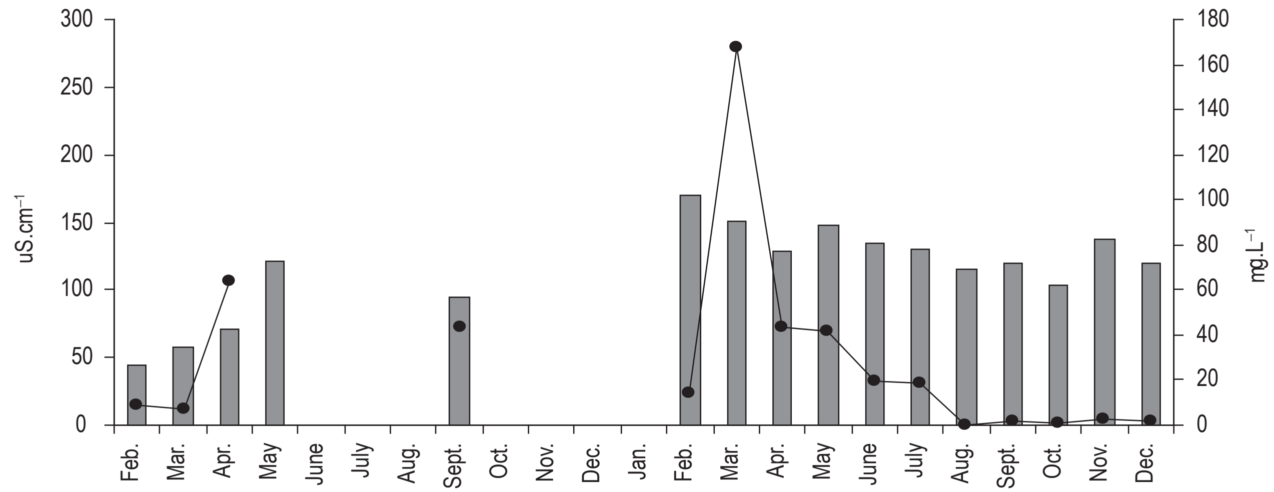

Figure 6. Electrical conductivity (µS cm^{-1}; bars) and, chlorophyll-a (µg L^{-1}; line) in Cavalos Lake from February 2000 to December 2001).

Table 2. Taxa richness of zooplankton in Cavalos Lake from March 2000 to December 2001 and, from the hatching experiment of resting eggs in sediment conducted in September, 2000.

Years	2000					2001										
Months	Mar.	Apr.	May	experiment	Sept.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Rotifera	15	5	8	9	4	3	26	16	23	21	16	10	19	12	16	13
Cladocera	7	7	3	4	2	2	4	2	1	3	3	2	3	0	4	2
Copepoda	3	3	2	1	3	2	3	2	1	4	2	6	5	3	3	3
TOTAL	25	15	13	14	9	7	33	20	25	28	21	18	27	15	23	18

Table 3. Relative abundance (%) of zooplanktonic groups in Cavalos Lake, from March 2000 to December 2001.

Years	2000				2001										
Months	Mar.	Apr.	May	Sept.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Rotifera	62.9	30.7	81.2	11.6	99.2	97.2	100.0	100.0	95.4	91.1	82.91	77.3	42.0	68.2	20.5
Cladocera	0.2	13.7	1.2	15.4	0.0	1.4	0.0	0.0	0.1	0.0	0.02	0.0	0.0	0.0	1.8
Copepoda	36.9	55.6	17.6	73.0	0.8	1.4	0.0	0.0	4.5	8.9	17.07	22.7	58.0	31.8	77.7

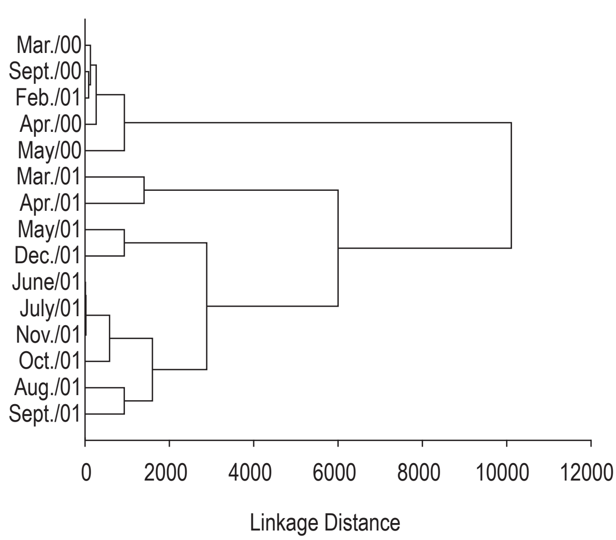

Figure 7. Grouping analysis by unweighted pair-group average (Euclidean distance) for the environmental variables measured in Cavalos Lake during the study period.

of months, especially in the first six months of lake recovery. The relative participation of Rotifera in community was overcome by Copepoda in April and September 2000 and in October and December 2001. Cladocera exceeded unusually 1% of relative abundance, except in April and September 2000 (relative abundance > 10 %).

Calanoida and Cyclopoida predominated for Copepoda, with alternated values before lake disappearance (Figure 8). In September 2000, Calanoida corresponded to 95 % of all the Copepoda, when the unique occurrence of Harpacticoida was recorded. After the lake recovery, Cyclopoida presented the highest relative abundance. Only in the two last months, Calanoida presented high relative participation, for both larvae stages and adult densities.

Densities of total zooplankton ranged from 12,000 to 1,750,000 $ind.m^{-3}$. Rotifera, Cladocera and Copepoda fluctuated in a same way as total zooplankton (Figure 9). Rotifera densities varied between 1,400 to 1,100,000 $ind.m^{-3}$. Cladocera occurred usually below 1,000 ind m^{-3}, except

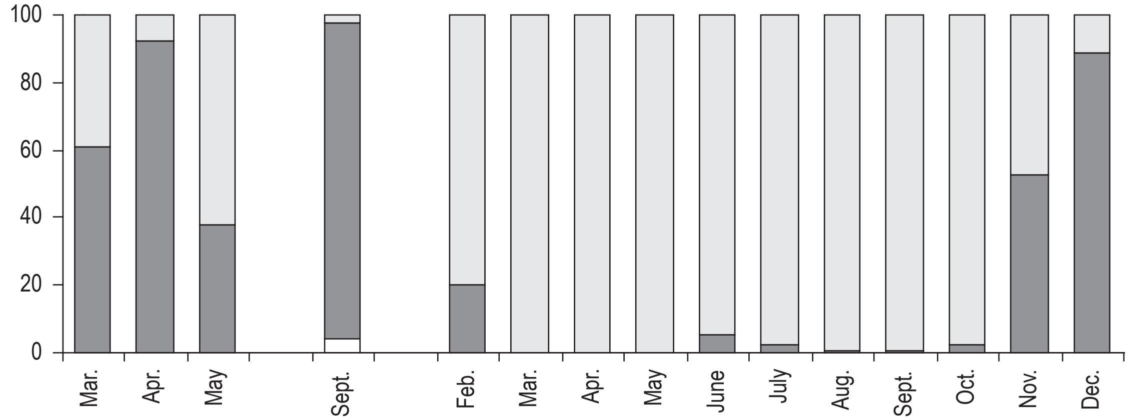

Figure 8. Ratios (%) between the densities of Copepoda Calanoida (black), Cyclopoida (gray) and Harpacticoida (white) of Cavalos Lake from March 2000 to December 2001.

in April 2000, when the density reached approximately 240,000 ind.m^{-3}.

Considering Copepoda, nauplii were numerically important (Figure 10), and the adults were more evident only in April 2000 and 2001. Absolute density of Calanoida nauplii ranged from 0 (February to May 2001) to 364,000 ind.m^{-3} (April 2000). In this last month, copepodids from Calanoida were also very abundant (218,000 ind.m^{-3}), and did not occur from March to August 2001; after that, their density increased continuously together with nauplii densities.

Experiment on resting eggs hatching evidenced that sediment of Cavalos Lake presented great numbers of dormant organisms. A higher number of individuals hatched from sediments where water content was high (sites P5 and P6). Number of hatchings increased exponentially along incubation time (Figure 11).

Higher number of hatching was recorded for Rotifera; only in the fourth and eighth incubation days, a greater number of Calanoida nauplii occurred. Cladocera hatchings were also detected, but usually in low number (Figure 12).

In the beginning of experiment, *Asplanchnopus* De Guerne, 1888 was an abundant taxa (the highest number was recorded in the fourth day: 20 individuals) but, it was found only up to the eighth day. *Lecane inermis* was found from the second day on and hatching number increased from the eighth to the last experiment day, when it was recorded 1,732 organisms.

Three species of Cladocera hatched: *Alona intermedia* Sars, 1862, *Ceriodaphnia cornuta* (Sars, 1886) and *Diaphanosoma birgei* (Korineck, 1981). *C. cornuta* was observed only in the fourth and eighth incubation days; *D. birgei* was found in a small number, however in a great number of days (sixth, fifteenth, twenty-ninth and fiftieth days); for *A. intermedia*, it was observed a high number of hatchings (59 individuals) but only between the twenty-ninth and forty-third incubation days.

Calanoida were the only organisms of Copepoda that hatched in a great number in the beginning of experiment. After that, the hatchings decreased continuously from the fifteenth day on, although detected up to the end of experiment.

Species diversity fluctuated from 0.80 (in Feb./01) to 3.42 bits.ind^{-1} (in May/01) (Figure 13). The highest values were found during the recovery of lake volume, after the drought period. On Sept./00, diversity was relatively high, when considered the low value of richness. This finding was attributed to the high value of equitability (Figure 13). Low equitability and richness produced a low value of diversity on Feb./01.

Cladocera and Copepoda densities presented a significant positive correlation ($p < 0.05$) to dissolved oxygen concentration, and negative to water electrical conductivity (Table 4). In relation to Cladocera, *Moina reticulata* Daday, 1905 showed negative correlation to dissolved oxygen concentration and, positive to water electrical conductivity as well as most of Rotifera species.

Some species presented high correlations with water transparency and suspended matter (Table 4). *Filinia terminalis* (Plate, 1886), *Polyarthra vulgaris* Carlin, 1943, *Trichocerca similis* (Wierzejski, 1893), *Kurzia polyspina* Hudec, 2000 and *Thermocyclops inversus* Kiefer, 1936 presented positive correlation with water transparency. However, this last variable and *Brachionus falcatus* Zacharias, 1898, *Epiphanes clavulata* (Ehrenberg, 1832) and *Moina micrura* (Kurz, 1874) densities showed negative correlations. For these three species, the correlation was positive with suspended organic matter and total pigments concentrations. Significant positive correlations with suspended inorganic matter were also observed for *Diaphanosoma birgei*, *Macrothrix squamosa* Sars, 1901 and *Notodiaptomus* Kiefer, 1936.

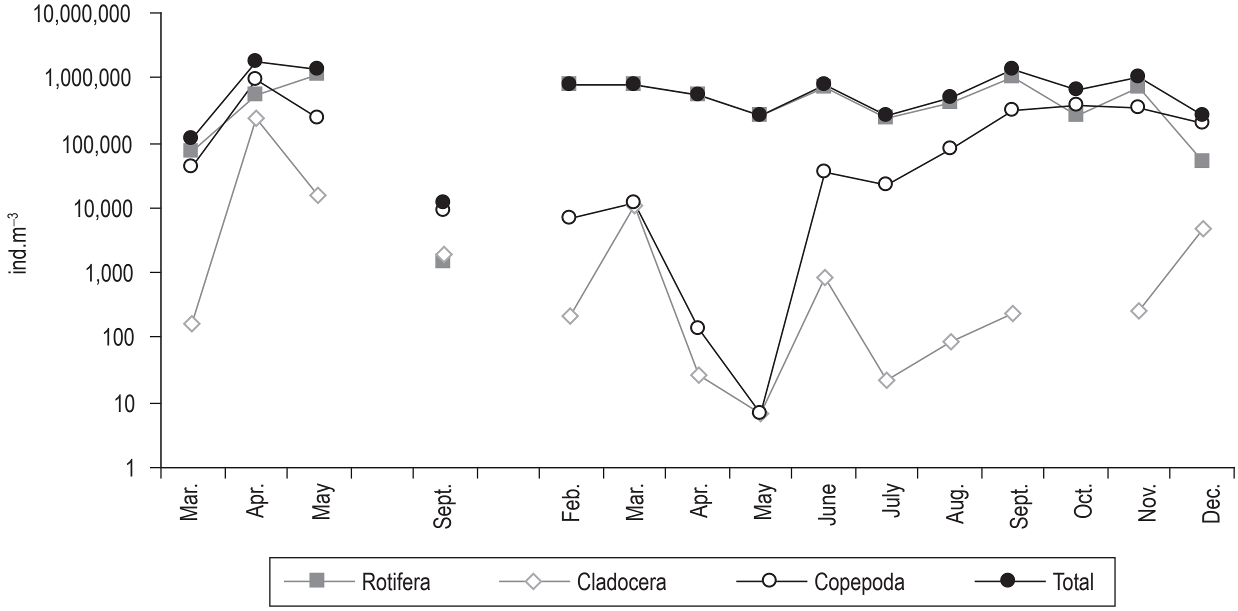

Figure 9. Absolute density (ind m^{-3}) of total zooplankton, Rotifera, Cladocera and Copepoda of Cavalos Lake from March 2000 to December 2001.

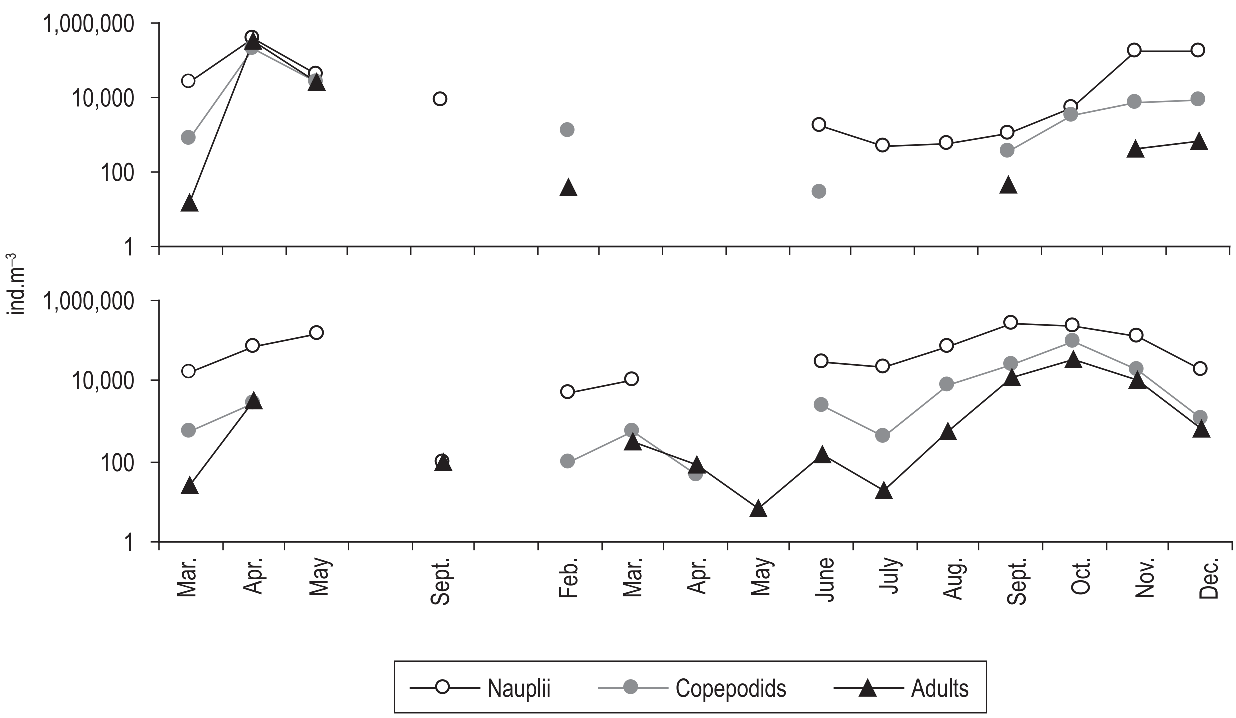

Figure 10. Absolute density (ind.m^{-3}) of nauplii, copepodids and adults of Calanoida (above) and Cyclopoida (below) of Cavalos Lake from March 2000 to December 2001.

Positive significant correlations were found between lake volume and densities of some species of Rotifera and, of *Moina reticulata* and *Thermocyclops decipiens* (Kiefer, 1926). Conversely, the abundance of *Diaphanosoma birgei*, *Macrothrix squamosa* and *Notodiaptomus* spp. presented a negative correlation with lake volume (Table 4).

Considering the four different phases, some species occurred in especial environmental conditions. Rotifera as *Colurella* Bory de St. Vincent., 1984, *Euchlanis* Ehrenberg, 1832, *Lecane closterocerca* (Schmarda, 1859), *L. curvicornis* (Murray, 1913) *L. elegans* Harring, 1914, *L. hamata* (Stokes, 1896), *Monommata* Bartsch, 1870, *Ptygura* Ehrenberg,

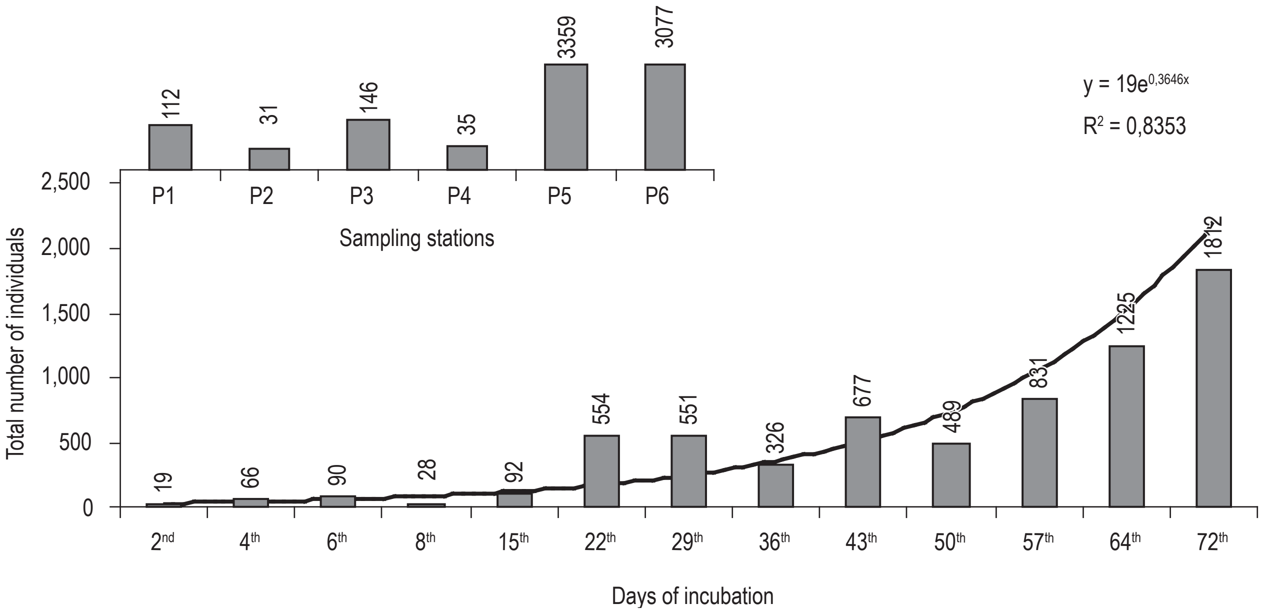

Figure 11. Total number of hatched organisms at sediment sampling sites in Cavalos Lake (above) and, by incubation time (below).

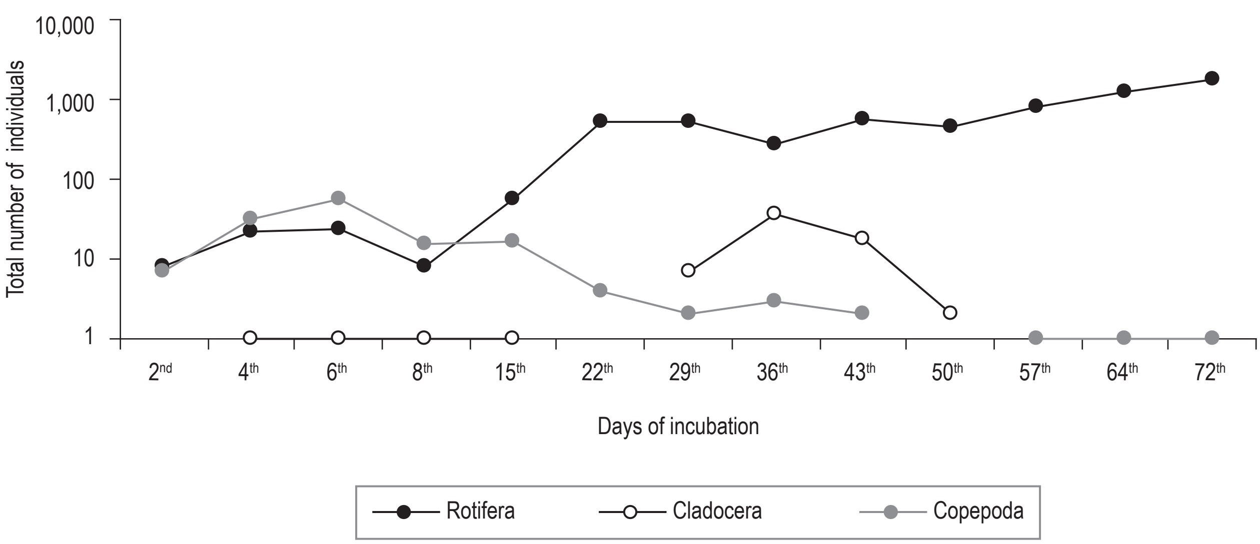

Figure 12. Total number of hatched organisms of the zooplanktonic groups during the incubation period.

1832, *Synchaeta pectinata* Ehrenberg, *A. pulchella* King, 1853, *Bosminopsis deitersi* Richard, 1895, *Kurzia polyspina* Hudec, 2000, *Chydorus* Leach, 1816 genus and *Metacyclops* Kiefer, 1927. were found in the high environmental stability situation. Only *C. cornuta rigaudi* and *Moina reticulata* were restricted to the high stress period. *Brachionus caudatus* Barrois and Daday, 1894, *Lecane* cf. *hastata* (Murray, 1913), *Bosmina hagmanni* Stingelin, 1904, *Diaphanosoma fluviatile* Hansen, 1899, *Macrothrix squamosa* Sars, 1901, *Scapholeberis armata* Herrick and Turner, 1895, *Eucyclops serrulatus* (Fischer, 1851) and *Paracyclops chiltoni* (Thomson, 1882) were registered only before the lake extinction (Table 5).

4. Discussion

Low rain precipitations, observed from October 1999 to December 2000 (Henry et al., 2005), reduced greatly the volume of Cavalos Lake, and allowed us to study the drought consequences on zooplankton. From Jan./01 on, the lake began to recover their condition of aquatic ecosystem, when it was observed the beginning of colonization by zooplanktonic populations.

Considering the abiotic characteristics, two periods can be identified: one involving high environmental stress, from the intense drought period and the first month of filling of the lake (from Mar./00 to Feb./01); the other, with a high hydrologic stability, corresponding to all the other months,

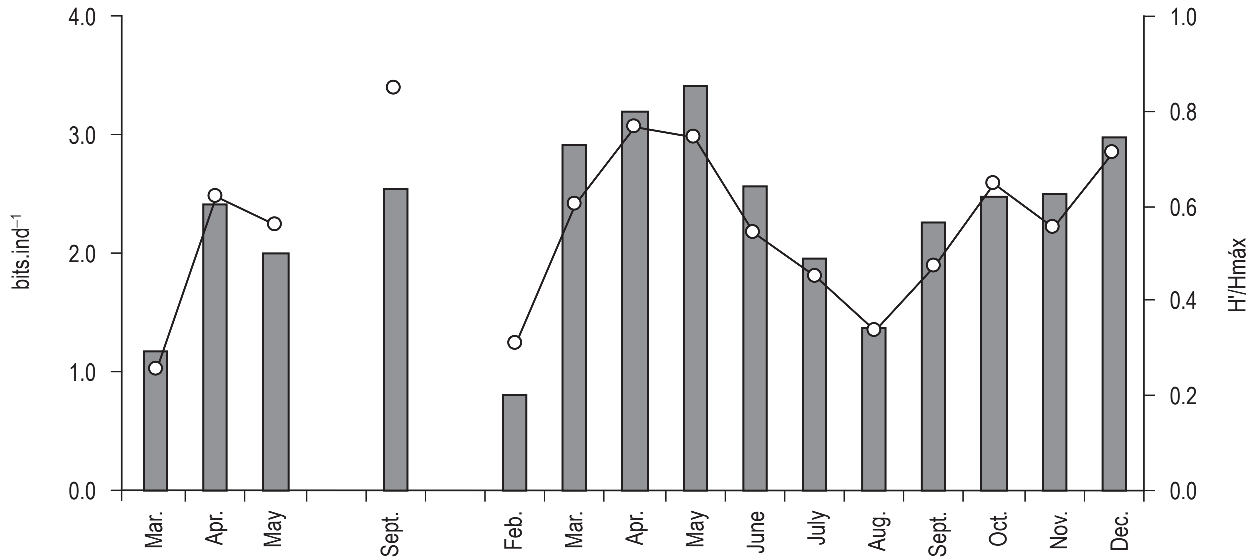

Figure 13. Species diversity (bits ind^{-1}; gray bars) and equitability (H'/Hmax – black line) of zooplanktonic community in Cavalos Lake from March 2000 to December 2001.

Table 4. Spearman correlations between environmental variables and densities of zooplankton species found in Cavalos Lake from March 2000 to December 2001 (DO, dissolved oxygen; EC, electric conductivity; SM, suspended matter; SOM, suspended organic matter; SIM, suspended inorganic matter; TP, total pigments).

	Temperature	DO	pH	EC	SM	SOM	SIM	Transparency	TP	Volume
A. fissa	-	-	-	-	-	-	-	-	0.38	-
Asplanchnidae	-	–0.56	-	0.52	-	0.37	-	-	-	0.66
Bdelloidea	-	–0.75	-	0.69	-	0.40	-	-	-	0.59
B. dolabratus	-	-	-	–0.34	-	-	-	-	-	-
B. falcatus	0.52	-	-	-	0.46	0.49	0.34	–0.34	0.46	-
B. quadridentatus	-	–0.52	-	0.48	-	0.33	-	-	0.33	0.57
E. clavulata	-	–0.46	-	0.48	0.44	0.56	0.33	–0.33	0.49	0.54
F. longiseta	-	–0.40	-	-	-	-	-	-	-	0.32
F. terminalis	–0.33	–0.33	-	0.40	-	-	–0.36	0.50	-	-
K. lenzi	-	-	-0.33	-	-	-	-	-	-	-
L. bulla	-	–0.61	-	0.55	-	0.37	-	-	0.34	0.66
P. patulus	-	-	-	-	-	-	-	-	-	0.40
P. vulgaris	-	-	-	-	–0.34	-	–0.45	0.56	-	-
T. similis	–0,71	-	-	-	–0.46	–0.41	–0.45	0.68	-	-
Rotifera	-	–0.38	-0.38	-	-	-	-	-	0.33	-
D. birgei	-	0.61	-	–0.66	0.47	-	0.57	–0.49	-	–0.59
D. brevireme	-	-	-	-	-	-	-	-	0.33	-
I. spinifer	-	-	-	–0.34	-	-	-	-	-	-
K. polyspina	–0.59	-	-	-	–0.37	–0.35	–0.31	0.40	-	-
M. squamosa	-	0.35	-0.41	-	0.42	0.37	0.50	–0.44	-	–0.34
M. micrura	-	-	-	-	0.56	0.60	0.49	–0.40	0.57	-
M. minuta	0.35	0.35	0.43	–0.36	-	-	-	-	-0.34	-
M. reticulata	0.51	–0.41	-	0.39	-	0.43	-	-	0.45	0.58
Cladocera	0.42	0.33	-	-	0.56	0.48	0.58	–0.56	-	-
Notodiaptomus sp.	-	0.52	-	–0.34	0.36	-	0.41	–0.33	-	–0.34
T. decipiens	-	-	-	-	-	-	-	-	-	0.44
T. inversus	-	-	-	-	-0.54	0.50	-0.60	0.55	-	-
Copepoda	-	0.46	-	–0.47	-	-	-	-	-	–0.40

characterized by high water volume in lake. However, in relation to community structure, four distinct phases were identified during the study, two in the intense drought period and, two during the period of high hydrologic stability. Beyond the changes on lake volume, variations on the limnological characteristics promoted modifications on community structure.

During the intense drought period, a first phase extending from March to May 2000 was characterized by great environmental alterations (increase on suspended matter concentration and, on electric conductivity; decrease on pH) due to the reduction on lake volume promoting a concentration effect on organisms. These changes on environmental characteristics enhanced probably the intra-zooplanktonic competition relationships. The phase from June 2000 to January 2001 corresponded to a period of organism latency, when the local community was inserted almost exclusively in egg banks. However, some hatching episodes occurred in this phase, when an ephemeral accumulation of water was observed after rain precipitation, as it was observed on Sept./00.

In the period of high hydrologic stability, the phase from Feb./01 to May/01 can be considered as the beginning of aquatic community recovery. In this phase, water transparency was firstly low, and high values of suspended organic matter, electric conductivity and total pigments, were found. Low values of dissolved oxygen were due to the intense degradation process of terrestrial vegetation, which was submerged. The high values of temperature increased the decomposition rates of organic matter. A second phase, extending from July to December 2001, corresponded to a recovery of more stable limnological conditions, with minor variations that can be compared to situation found by Martins and Henry (2004), before the intense drought.

Considering all the knowledge on zooplankton of Cavalos Lake (Martins and Henry, 2004; this study), 110 taxa were recorded, 90 taxa during this study and 64 taxa were observed by Martins and Henry (2004). In the intense drought phase, the richness was reduced to 39 taxa. An increase to 49 taxa was recorded in the beginning of lake recovery, and the highest richness of zooplankton (67 taxa) was found during the period extending from June to December 2001, when Cavalos Lake presented more stable hydrologic conditions.

When considered the period before and after the lake extinction, data showed that an increase on Rotifera richness (from 42 to 51) occurred, a decrease on taxa number of Cladocera (26 and 12 species before and after the drought period, respectively). Copepoda presented no change on species richness (8 taxa),but only a modification on the species composition was observed.

Eucyclops serrulatus (Fischer, 1851) and *Paracyclops chiltoni* (Thomson, 1882), as well as some Cladocera species, were registered only before the lake extinction. According to Frisch (2002), *E. serrulatus* does not present dormancy phase in environments that dried completely, and the capacity to remain in wetland lakes is related to its dispersion capacity. Probably, *P. chiltoni* presented no resting eggs in sediment and, the lack of connection between river and lake during the study period can explain the absence of some species after the drought.

On September 2000, richness was low, being the community composed by organisms that began their activity fastly, few hours after water accumulation in lake. Relatively high diversity, despite low richness, was attributed to reduced time of water accumulation that restrained dominance relations in the community.

The renewal of resting eggs stock in a short-term was also observed by Crispim and Watanabe (2000) in a reservoir of semi-arid region of state of Paraíba (Brazil). In this system, favorable conditions to active life for some Rotifera species were produced after the rains. However, other species hatched, multiplied, and produced new resting eggs and died after that, renewing the resting eggs stock in sediment.

Low number of taxa hatched during the experiment, when compared to the richness of zooplankton in Cavalos Lake. Stable experimental conditions in laboratory probably affected the hatching of low number of species. In the lake, the environmental variability promoted different conditions for hatching of eggs after lake recovery. Sampling depth of sediment can also affect the number of hatchings (Hairston et al., 1995). Considering that sediment sampling was limited to surface in this study, only organisms recently in dormancy hatched during the experiment.

Variables related to trophic conditions of water presented significant correlations with the density of zooplanktonic taxa. Densities of *Diaphanosoma birgei*, *Moina minuta* and *Notodiaptomus* spp. increased with higher dissolved oxygen concentrations and low values of water electric conductivity. *M. minuta* presented negative correlation with total pigments, while *M. micrura* showed positive correlation with total pigments and with organic matter concentration. Despite that *Moina* species presented distinct correlations with some environmental variables, as total pigments, *M. micrura* occurred together with two other congeneric species. However, co-existence of *M. minuta* and *M. reticulata* was not observed during all the study.

Densities of *M. reticulata* and some Rotifera species (as Asplanchnidae, Bdelloidea, *Brachionus quadridentatus* Ehrenberg, 1832, *Epiphanes clavulata* and *Lecane bulla* (Gosse, 1851)) increased when more eutrophic conditions (identified by high electric conductivity and low dissolved oxygen, suspended organic matter and total pigments concentrations) and higher water volumes were reached. Frutos (1996) related also *Epiphanes*, *Lecane* and *Filinia* taxa with low concentrations of dissolved oxygen in Turbia lagoon

Table 5. Zooplankton species of Cavalos Lake recorded in different periods of study.

Taxa	2000			2001	
	1st Phase	2nd Phase		3rd Phase	4th Phase
	Mar.-May	Hatching	Sep.	Feb.-May	June-July
Anuraeopsis fissa				x	x
Asplanchnidae	x	x		x	x
Ascomorpha spp.				x	x
Bdelloidea	x	x		x	x
Brachionus angularis				x	x
B. bidentata				x	x
B. caudatus	x				
B. dolabratus	x			x	
B. falcatus	x	x		x	
B. mirus				x	
B. quadridentatus				x	x
Cephalodella sp.	x	x		x	x
Collotheca spp.			x	x	x
Colurella sp.					x
Conochilus coenobasis				x	x
Dicranophorus sp.	x				x
Dipleuchlanis sp.				x	
Epiphanes clavulata				x	x
Euchlanis spp.					x
Filinia longiseta				x	x
F. opoliensis				x	x
F. terminalis				x	x
Gastropus stylifer				x	x
Hexarthra spp.				x	x
Keratella americana		x			x
K. cochlearis	x				x
K. lenzi	x				x
K. tropica	x				x
Lecane spp.	x			x	x
L. bulla				x	x
L. closterocerca					x
L. curvicornis					x
L. elegans					x
L. cf. *furcata*				x	x
L. hamata					x
*L.*cf. *hastata*	x				
L. hornemani				x	x
L. cf. *inermis*		x			
L. luna	x			x	x
L. lunaris					x
L. papuana	x			x	x
L. cf. *pyriformis*	x				x
Lepadella spp.	x			x	x
Mytilina spp.	x			x	x
Monommata spp.					x
Philodina		x			
Plationus patulus				x	x
Platyias quadricornis				x	x
Polyarthra vulgaris	x		x	x	x
Pompholix sulcata		x	x		
Ptygura sp.					x
Synchaeta pectinata					x
S. stylata	x		x		
Testudinella brycei	x				
Testudinella patina				x	
Trichocerca spp.	x	x		x	x
T. dixon-nutali				x	x
T. similis				x	
Trichotria sp.				x	x
Total Rotifera	**21**	**9**	**4**	**36**	**46**
Alona pulchaella					x
Alona intermedia	x	x			
Bosmina hagmanni	x				
B. longirostris			x		
Bosminopsis deitersi					x
Ceriodaphnia cornuta		x			
C. cornuta rigaudi	x			x	
C. silvestrii		x			
Chydorus sp.					x
C. pubescens					x
D. birgei	x	x	x		
D. brevireme	x			x	x
D. fluviatile	x				
D. spinulosum				x	
Ilyocryptus spinifer	x				x
Kurzia polyspina					x
Macrothrix squamosa	x				
Moina micrura	x			x	x
M. minuta	x				x
M. reticulata				x	
Scapholeberis armata	x				
Total Cladocera	**11**	**4**	**2**	**5**	**9**
Notodiaptomus spp.	x	*	*	x	x
Eucyclops serrulatus	x				
Mesocyclops spp.	x				x
M. longisetus				x	x
Metacyclops mendocinus					x
Microcyclops anceps	x				x
Paracyclops chiltoni	x				
Thermocyclops decipiens				x	x
T. inversus			x	x	x
Harpacticoida			x		
Total Copepoda	**5**	**1**	**3**	**3**	**6**
Total	**37**	**14**	**9**	**44**	**61**

* nauplii of Calanoida

1st Phase: Mar - May/00 – before the drought;

2nd Phase: Hatching – data from hatching experiment in laboratory; Sept./2000 – rain episode during the drought;

3rd Phase: Feb-May/01 – initial phase of recovery;

4th Phase: June-Dec./01 – phase of high hydrologic stability of the lake.

(Argentina) during the high water period and, considered these three species tolerant to low oxygen concentrations.

Diaphanosoma birgei, *Macrothrix squamosa* and *Notodiaptomus* spp. presented a negative correlation with the lake volume and positive with suspended inorganic matter, indicating that these species can be enhanced in shallow environments with high water mixing.

Thermocyclops decipiens densities showed positive correlation with volume, while *T. inversus* presented positive correlation with water transparency and negative with suspended inorganic matter, especially in the period of high water transparency, when *T. inversus* density was higher than *T. decipiens* abundance. When the two species reappeared in March, in function of dormancy interruption, *T. decipiens* was more abundant. Nevertheless, from Aug./01 on, the environmental conditions enhanced the population increase of *T. decipiens*. According to Frisch (2002), the dormancy of some species of Cyclopoida is a way to resist to drought but it is also a strategy to escape to predation and lack of food.

Notodiaptomus, the only Calanoida, hatched in relatively high number in September 2001 and presented the highest number of hatchings in the first eight days. Up to the end of experiment, the number of hatchings of Calanoida nauplii was reduced. In the four months after the lake recovery, Calanoida presented a very low number, but a considerable increase was observed up to the end of study.

The Calanoida organisms seem to have no tolerance to eutrophic conditions and to high variability in aquatic environment. In Cavalos Lake, this group was recorded before the lake extinction, when it probably renewed the stock of resting eggs, and increased proportionally in number, with time, after the lake recovery. Another probable explanation to the slow colonization of these organisms can be the presence of resting eggs in deeper layers of sediment and, in the littoral region of lake. The deepest sediment, presenting resting eggs, was probably re-suspended after greater hydration time, and mixing in water column.

Hairston et al. (1995) found viable eggs of *Diaptomus sanguineus* in Bullhead Pond (Rhode Island, USA) in sediment up to 30 cm depth and estimated an average age for hatching of around 70 years. According to a revision made by Crispim et al. (2003), Cladocera eggs can remain viable up to 55 years and, resting eggs of Rotifera, up to 35 years. However, Crispim and Watanabe (2000), after a study in the littoral zone of a reservoir of the semi-arid region of Brazil, concluded that the viability of Rotifera eggs could support no more than 13 years of drought. This difference can be a characteristic of the considered Rotifera species. However, it must be emphasized that available data on resting eggs of planktonic organisms were, in most cases, produced in temperate regions and the viability of restings eggs in driest regions, where ecological processes presented high intensity, was not well evaluated yet.

Cyclopoida appeared in a low number after the drought, and increased in density up to October, when it was observed a reduction together with an increase on Calanoida. In addition, its resting eggs did not hatch during the experiment. More stable hydrologic condition and oligotrophy of environment enhancing a high development of Calanoida when compared to Cyclopoida were also observed by Nogueira (2001) and Panarelli et al. (2003), in a study on spatial distribution of Calanoida and Cyclopoida in Jurumirim Reservoir (São Paulo, Brazil).

Studies on resting organisms can help to understand the dynamics of communities in temporary lakes and wetlands, since sediment of aquatic ecosystems, with great variation on inundation area or significant changes on water physical and chemical characteristics, can present a great number of species maintained as resting eggs, supporting a higher richness than the water column.

Brendonck and Williams (2000) related the highest species richness to duration of hydro-period and to the large area of inundation in several types of wetlands. Diversity values, due to high taxa richness in Cavalos Lake, were not clearly related to great duration of inundation, but presented a tendency to increase in high water period, when the inundated area of lake was bigger.

When compared to other lakes of wetlands (Paggi and José de Paggi, 1990; Campos et al., 1996; Espíndola et al., 1996; Guntzel et al., 2000; Rocha et al., 2000; Wisniewski et al., 2000), Cavalos Lake presented a relatively high richness, mainly considering its low dimensions and the relatively spatial homogeneity. This finding can be related to high frequency of sampling (four years, including the data of Martins and Henry, 2004), that allowed us to show patterns of temporal heterogeneity, involving species found during the year, but also species that many times remain in dormancy and contribute actively only in stress situations, consequence of a great environmental disturbance, as it was the severe drought in Cavalos Lake.

In Cavalos Lake, the resting eggs had an important role on the recovery of the zooplankton diversity after drought, since no organisms from the river was introduced in this isolated aquatic environment, during the falling period. Despite that the zooplankton community observed after the drought was derived from resting eggs of a preexistent community, notable differences were recorded between the two periods. An increase on Rotifera richness, a decrease on Cladocera richness and density and, a change in the Calanoida and Cyclopoida ratios were the main modifications.

Acknowledgements

This work was supported by FAPESP (Proc.: 99/08748-5 and 97/04999-8) and CNPq (Proc.: 141360/2000-2003). The authors are grateful to Hamilton A. Rodrigues and Lúcio Miguel de Oliveira for field assistance.

References

BEGON, MJ, HARPER, L. and TOWNSEND, CR. *Ecology: Individuals, populations and communities.* 3rd ed. Oxford: Blackwell Science, 1996.

BRENDONCK, L. and WILLIAMS, WM. *Biodiversity in wetlands of dry regions (drylands).* In GOPAL, B., JUNK,WJ. and DAVIS, JA. (eds). Biodiversity in wetlands: assessment, function and conservation. 2000.

BROCK, MA., NIELSEN, DL., SHIEL, RJ., GREEN, JD. and LANGLEY, JD. Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. *Freshwater Biology,* 2003, vol. 48, p.1207-1218.

CAMPOS, JRC., LANSAC-TÔHA, FA., NUNES, MA., GARCIA, APP. and PRADO, FR. Composição da comunidade zooplanctônica de três lagoas da Ilha Porto Rico na planície de inundação do Alto Rio Paraná. *Acta Limnologica Brasiliensia,* 1996, vol. 8, p. 183-194.

CHATTERJEE, K. and GOPAL, B. Experimental study of emergence of zooplankton in temporary water-bodies in relation to dry periods. *Verhandlungen der Internationalen Vereinigung der Limnologie,* 1998, vol. 26, p. 1309-1315.

COLE, GA. *Textbook of limnology*. 2nd ed. Saint Louis: The C.V. Mosby Company, 1979.

CRISPIM, MC. and WATANABE, T. Ovos de resistência de rotíferos presentes em sedimentos secos de um açude no semi-árido paraibano. *Acta Limnologica Brasiliensia*, 2000, vol. 12, p. 89-94.

CRISPIM, MC., DA PAZ, RJ. and WATANABE, T. Comparison of different *Moina minuta* populations dynamics ecloded from resting eggs in a semi-arid region in Brazil. *Brazilian Journal of Ecology,* 2003, vol. 1, p. 33-38.

DE STASIO, BT. The seed bank of a freshwater crustacean: copepodology for the plant ecologist. *Ecology,* 1989, vol. 70, p. 1377-1389.

DE STASIO, BT. The role of dormancy and emergence patterns in the dynamics of a freshwater zooplankton community. *Limnology and Oceanography,* 1990, vol. 35, p. 1079-1090.

ESPINDOLA, EG., MATSUMURA-TUNDISI, T. and MORENO, IH. Efeitos da dinâmica hidrológica do sistema Pantanal Matogrossense sobre a estrutura da comunidade de zooplâncton da lagoa Albuquerque. *Acta Limnologica Brasiliensia,* 1996, vol. 8, p. 37-57.

FRISCH, D. Dormancy, dispersal and the survival of cyclopoid copepods (Cyclopoida, Copepoda) in a lowland floodplain. *Freshwater Biology,* 2002, vol. 47, p. 1269-1281.

FRUTOS, SM. Zooplancton de la Laguna Turbia (Isla del Cerrito) en la conffluencia de los Rios Parana y Paraguay (Argentina). *Revista Brasileira de Biologia,* 1996, vol. 56, p. 569-580.

GOLTERMAN, HL., CLYMO, RS. and OHMSTAD, MA. *Methods for physical & chemical analysis of freshwaters.* IBP N.8. 2nd ed. Oxford: Blackwell Scientific Publications, 1978.

GUNTZEL, AM., ROCHA, O., ESPINDOLA, EG. and RIETZLER, AC. Diversidade do zooplâncton nas lagoas marginais do rio Mogi-Guaçu: I. Rotifera. *In* SANTOS, JE. and PIRES, JSR. (Eds). *Estação Ecológica de Jataí*. São Carlos: RiMa, 2000. vol 2, cap. 16, p. 537-557.

HAIRSTON, NG., VAN BRUNT, RA. and KEARNS, CM. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology*, 1995, vol. 76, p. 1706-1711.

HARPER, JL. *Population Biology of Plants*. London: Academic Press, 1997.

HENRY, R. The connectivity of the Paranapanema River with two lateral lakes in its mouth zone into the Jurumirim Reservoir. *Acta Limnologica Brasiliensia,* 2005, vol. 17, p. 57-69.

HENRY, R., PANARELLI, EA., CASANOVA, SMC., SUIBERTO, MR., AFONSO, AA. de O. Interações hidrológicas entre lagoas marginais e o rio Paranapanema na zona de sua desembocadura na represa de Jurumirim. In: NOGUEIRA, MG., HENRY, R. and JORCIN, A. (eds). *Ecologia de reservatórios*: impactos potenciais ações de manejo e sistemas em cascata. São Carlos : RiMa, 2005. p.57-82.

KOSTE, W. *Rotatoria - Die Redertiere Mitt Leuropas* - I Text Band. 1978a. 237 p.

KOSTE, W. *Rotatoria - Die Redertiere Mitt Leuropas* - II Text Band. 1978b. 237 p.

KREBS, CJ. *Ecological Methodology*. 2nd ed. New York: Benjamin/ Cummings, 1999. 620 p.

El-MOOR LOUREIRO, LMA. *Manual de identificação de cladóceros límnicos do Brasil.* Brasilia: Universa, 1997. 156 p.

MARTINS, GM. and HENRY, R. Composição e abundância do zooplâncton em três lagoas laterais ao Rio Paranapanema na zona de sua desembocadura na represa de Jurumirim (São Paulo). In CHELAPPA, S. and PASSAVANTE, JZO. (Eds). *Ecologia Aquática Tropical.* Natal: ServGraf Editor, 2004. p. 53-72.

NOGUEIRA, MG. Zooplankton composition, dominance and abundance as indicator of environmental compartmentalization in Jurumirim reservoir (Paranapanema River), São Paulo, Brazil. *Hydrobiologia,* 2001, vol. 455, p. 1-18.

PAGGI, JC. and JOSE DE PAGGI, S. Zooplâncton de ambientes lóticos e lênticos do Rio Paraná Médio. *Acta Limnologica Brasiliensia,* 1990, vol. 3, p. 685-719.

PANARELLI, EA., CASANOVA, SMC., NOGUEIRA, MG., MITSUKA, PM. and HENRY, R. A comunidade zooplanctônica ao longo de gradientes longitudinais no Rio Paranapanema/Represa de Jurumirim (São Paulo – Brasil). In HENRY, R. (ed.). *Os ecótonos nas interfaces dos ecossistemas aquáticos.* São Carlos: Editora RiMa, 2003. p.129-160.

PONTIN, RM. *Freshwater planktonic and semi-planktonic Rotifera of the British Isles*. Freshwater Biological Association Scientific publication no 38, 1978. 178p.

REID, JW. Chave de identificação e lista de referências bibliográficas para as espécies continentais sulamericanas de vida livre da ordem Cyclopoida (Crustacea, Copepoda). *Bolm. Zool.,* 1985, vol. 9, p.17-143.

ROCHA, O. and MATSUMURA-TUNDISI, T. *Atlas do zooplâncton (Represa do Broa, São Carlos) Vol. I - Copepoda.* Centro de Ciências e Tecnologia, Departamento de Ciências Biológicas, Universidade Federal de São Carlos, 1976. 68 p.

ROCHA, O., ESPINDOLA, EG., RIETZLER, AC. and WISNIEWSKI, MJS. Diversidade do zooplâncton nas lagoas marginais do rio Mogi-Guaçu: III. Copepoda (Crustacea). In SANTOS, JE. and PIRES, JSR. (eds). *Estação Ecológica de Jataí* (vol. 2). São Carlos: RiMa, 2000. p. 587-598.

VON SPERLING, E. *Morfologia de lagos e represas*. Belo Horizonte: DESA/UFMG, 1999.

WISNIEWSKI, MJS., RIETZLER, AC. and ESPINDOLA, EG. Diversidade do zooplâncton nas lagoas marginais do rio Mogi-Guaçu: II. Cladocera (Crustacea). In SANTOS, JE. and PIRES, JSR. (eds). *Estação Ecológica de Jataí* (vol. 2). São Carlos: RiMa, 2000. p. 559-586.

Received: 23 January 2008
Accepted: 26 May 2008